

SELF-FERTILIZATION AND HERBIVORY IN A RARE ALPINE PLANT IN CALIFORNIA, *CLAYTONIA MEGARHIZA* (MONTIACEAE)

DENA GROSSENBACHER*

California Polytechnic State University, Biological Sciences Department, 1 Grand Ave., San Luis Obispo, CA 93407 dgrossen@calpoly.edu; University of California, Davis, Department of Evolution and Ecology, One Shields Ave., Davis, CA 95616

RYAN BRISCOE RUNQUIST*

University of California, Davis, Department of Evolution and Ecology, One Shields Ave., Davis, CA 95616; University of Minnesota, Department of Plant and Microbial Biology, 140 Gortner Laboratory, 1479 Gortner Ave., St. Paul, MN 55108

JOEL SMITH

University of California, Davis, Department of Evolution and Ecology, One Shields Ave., Davis, CA 95616; University of Chicago, Department of Ecology and Evolution, 1101 E. 57th Street, Chicago, IL 60637

ABSTRACT

Reproduction in alpine habitats is challenging because of the short growing season, low temperatures, and high winds. This predicts alternative strategies for sexual reproduction in plants: compensatory measures such as larger floral displays and greater floral longevity to attract scarce pollinators and maintain outcrossing, or high levels of autonomous self-fertilization to assure reproduction in the absence of reliable pollinators. Here, we assessed the roles of animals (crawling insects, flying insects, and vertebrates) on the reproductive success of *Claytonia megarhiza* (A. Gray) S. Watson (alpine spring beauty). We measured fruit set and leaf herbivory while excluding animals from individual plants at a single site in Yosemite National Park, California. We found that plants were capable of setting fruit in the absence of pollinators and that, in the presence of animals, there was a 42% reduction in fruit set and a 159% increase in leaf damage. This suggests that *Claytonia megarhiza* may reproduce primarily by self-fertilization, and that herbivory may limit the reproductive success of this species near its southern range edge in California.

Key Words: ant, breeding system, mating system, outcrossing, pollination, reproductive assurance, selfing, geographic range edge.

The reproductive biology of California's alpine plant species is poorly characterized compared to other alpine regions of the world (Körner 2003), and yet is of fundamental importance for colonization, establishment, and long-term persistence of populations and species (Schemske et al. 1994). The severity of the alpine environment—short growing season, low temperatures, intense solar radiation and strong winds—makes reproduction particularly challenging (Billings and Mooney 1968). Pollinator diversity and abundance in alpine habitats is typically limited (Billings and Mooney 1968; Bingham and Orthner 1998; Sandvik et al. 1999; Arroyo et al. 2006), and herbivore pressures can be intense (e.g., Spira and Pollak 1986; Galen 1990, 1999). Furthermore, because many of California's alpine plant species are rare (California Native Plant Society, Rare Plant Program 2016), and because alpine habitat is predicted to decrease by 50–90% across California by 2100 (Hayhoe et al. 2004), there is an urgent need to improve our understanding of the reproductive biology of California's alpine species.

Low pollinator diversity and abundance in alpine habitats favor alternative, but not mutually exclusive, pollination strategies. Plant species may evolve to have large, synchronous floral displays and increased floral longevity, which may improve the odds of successful pollination in pollinator-limited environments (e.g., Bingham and Orthner 1998; Blionis et al. 2001). In addition, alpine plants may rely on animals that are typically inefficient pollinators but are abundant in alpine habitats, such as flies and even ants (e.g., Stanton and Galen 1989; Puterbaugh 1998). Conversely, uniparental reproduction may be favored in the alpine (e.g., Spira and Pollak 1986; Gómez 2002; Zhang and Li 2008), by increasing reproductive success in the absence of reliable pollinators. This may be achieved through fertilization of ovules with self pollen (self-fertilization), or through asexual reproduction (e.g., apomixis). Over time, pollinator-limited populations may evolve to be mixed mating, predominantly self-fertilizing, or asexual, allowing for rapid reproduction and reduced investment in traits associated with pollinator attraction (Sicard and Lenhard 2011). Yet, despite the potential benefits of uniparental reproduction, it also incurs costs, such as reduced genetic variation and

* Both authors contributed equally to this work



FIG. 1. *Claytonia megarhiza* is distributed in mountainous regions of western North America (left panel: white filled circles represent locations of voucher specimens, grey filled diamond indicates the study site in Yosemite National Park). Growth habit (upper and lower right) with nectaring *Formica* ant (lower right inset) near the study site in Yosemite National Park.

the accumulation of harmful mutations (reviewed in Wright et al., 2013). These costs may negatively impact a population's ability to adapt to changing environments and limit long-term population persistence (Stebbins 1957; Igic and Busch 2013). Thus, conservation strategies will differ depending on the extent to which a population or species depends on uniparental reproduction.

In addition to pollination, herbivory is another way in which animals impact plant reproduction in alpine habitats. For example, herbivory by marmots was found to limit sexual reproduction in *Gentiana newberryi* A. Gray in the White Mountains of California, and is hypothesized to favor delayed flowering until after marmots have initiated hibernation in late summer (e.g., Spira and Pollak 1986). Similarly, Galen (1990, 1999) found that phloem-feeding insects, ungulates, and ants can all limit reproduction in *Polemonium viscosum* Nutt. (alpine skypilot) in the Rocky Mountains of North America. In particular, pollinating bumblebees and flower-destroying ants exerted opposing effects on reproduction (Galen and Geib 2007). It is thus important to consider both potential pollinators and herbivores

when assessing the reproductive success of alpine plants.

Here, we assess the impact of potential pollinators and herbivores on the reproduction of an alpine plant in California – *Claytonia megarhiza* (A. Gray) S. Watson. *Claytonia megarhiza* is a perennial species that is widely distributed throughout the Rocky Mountains and the Cascades with disjunct populations in the Canadian arctic and New Mexico (Fig. 1). In California, it reaches its southern extent in the central Sierra Nevada where there are 14 documented occurrences inside Yosemite National Park. It has broad, fleshy, basal leaves and a long, stout taproot, with reports of taproots more than two meters long (Zwinger and Willard 1996). Plants only reproduce via flowers, with no vegetative reproduction. Flowers are 12–20 mm in diameter with white, pink, or rose petals (Baldwin et al. 2012). *Claytonia megarhiza* occurs in rock crevices and on loose talus, scree, or gravelly slopes, primarily in alpine habitats above treeline (Miller and Chambers 2006). In the Yosemite region, it is restricted to north facing slopes that hold snow accumulation late into summer and may thus be impacted by diminished snowpack predicted

under most climate change scenarios (Hayhoe et al. 2004). *Claytonia megarhiza* is listed by the California Native Plant Society as rare, threatened or endangered in California, but is common in other portions of its range (Rank 2B.3 in California Native Plant Society, Rare Plant Program 2016).

The reproductive biology of *Claytonia megarhiza* is poorly understood. Close relatives vary in their dependence on pollinators. *Claytonia virginica* L. relies heavily on pollinator visitation for successful reproduction [although there are reports of self-compatibility and self-fertilization of fruits at very low levels (Schemske 1977; Morgan 1998)], while *C. perfoliata* undergoes autonomous self-fertilization (Miller and Chambers 2006). There are no known reports of floral visitors to *C. megarhiza*, but ants of the genus *Formica* have been observed on flowers in Yosemite National Park (Fig. 1, Grossenbacher, pers. obs.). Because ants are generally inefficient pollinators and sometimes act as herbivores (Galen and Geib 2007), it is unclear whether they provide a net benefit or detriment to reproduction in *C. megarhiza*.

Here, we experimentally assessed the impact of animals (ants and other crawling insects, flying insects, and vertebrates) on successful reproduction of a single population in Yosemite National Park. We addressed three primary study questions: 1) Is *Claytonia megarhiza* capable of autonomous self-fertilization?, 2) Do animals positively or negatively impact fruit set and leaf damage?, and 3) In particular, do ants and other crawling insects positively or negatively impact fruit set and leaf damage, i.e., do they act as pollinators, herbivores, or both?

METHODS

Study Design

This study took place in Yosemite National Park in a *C. megarhiza* population near Ireland Lake in Tuolumne Co., CA above tree line on a NW facing granitic slope (ca. 3450–3480 m elevation, 37.775661 latitude, –119.292286 longitude). On 26 July 2008, we established three 30 m transects, each approximately 15 m apart running NE to SW (i.e., perpendicular to the NW facing slope). The three transects act as blocking factors to sample the naturally occurring elevational gradient in the experimental site (roughly 30 m elevational change). Along each transect, we identified 25 focal plants by choosing the first 25 plants that were at least 5 cm in diameter and within 0.5 m of the transect tape. We then randomly assigned five focal plants along each transect to each of the following five treatments ($n = 5$ plants/treatment/transect):

No treatment. Plants were marked with a small removable metal tag but received no treatment. This

allowed us to assess natural levels of fruit-set and herbivory.

All animals excluded. Plants were enclosed in a clear plastic flashing collar covered with netting (0.5 mm hole diameter). This mesh size effectively excludes most insects and all vertebrates, such as yellow-bellied marmots which were common at this site (Grossenbacher personal observation). We also applied the product Tree Tanglefoot (hereafter “Tanglefoot”, The Tanglefoot Company, Grand Rapids, MI) to further prevent access by crawling insects. Tanglefoot is a commercial product that provides a sticky surface that crawling insects cannot cross. This treatment tested whether excluding all potential pollinators and herbivores had an effect on fruit-set and herbivory, and specifically tested for autonomous self-fertilization.

Crawling insects excluded. Plants were enclosed in a plastic flashing collar and Tanglefoot was applied to impede access by ants and other crawling insects. Flying insects and vertebrates still had access to the plants. This treatment tested whether excluding crawling insects had an effect on fruit-set and herbivory.

Control A. To evaluate the effect of plastic flashing, plants were enclosed in a plastic flashing collar, but no Tanglefoot or netting was applied. This allowed all potential pollinators and herbivores to access plants, and tested whether flashing had an effect on fruit-set and herbivory. For example, the roughly 4 cm tall flashing may act as a wind barrier, influencing air flow and temperature around plants.

Control B. To evaluate the effect of netting, plants were enclosed in a plastic flashing collar covered with netting, with holes cut in the netting. This allowed all potential pollinators and herbivores to access the plants and tested whether the shade created by netting had an effect on fruit-set and herbivory.

Treatments were implemented on 26 July 2008 immediately after snowmelt. When flowering was complete for nearly all plants (i.e., there were no new developing flowers or inflorescences), we censused the population (9 September 2008). We assessed reproductive success by counting the number of set fruits per plant, which equaled the sum of undehisced and dehisced capsules. To estimate plant size and herbivore damage, we counted the total leaf number per plant, and estimated the amount of herbivore damage by visually surveying leaves for damage. A leaf was categorized as herbivorized if greater than 25% of the surface was missing or damaged (evidence of insect sucking or chewing scars or browsing). We used the remaining leaf margins to estimate the original leaf size and therefore the percent damage. For each individual plant, the percent leaf damage was equal to the number of damaged leaves divided by the total leaf number per plant.

TABLE 1. FRUIT SET AND PERCENT LEAF DAMAGE AS RESPONSE VARIABLES IN TWO SEPARATE GENERALIZED LINEAR MODELS (A), AND THEIR ASSOCIATED PRE-PLANNED CONTRASTS (B). “F” indicates F value, “z” indicates Z value, and subscript “df” indicates the degrees of freedom.

(A) Overall model	Fruit set		Percent leaf damage	
	F _{df}	P	F _{df}	P
Source of variation				
Exclusion treatment (5 levels)	2.22 ₄	0.078	3.75 ₄	0.008
Transect (3 levels)	2.86 ₂	0.065	4.73 ₂	0.012
Exclusion treatment X transect	0.49 ₈	0.857	2.48 ₈	0.022
(B) Pre-planned contrasts	Z _{df}	P	Z _{df}	P
Source of variation				
All animals excluded versus all other treatments	2.71 ₁	0.007	−3.61 ₁	<0.001
Crawling insects excluded versus No treatment, Control A, and Control B	1.16 ₁	0.245	−0.39 ₁	0.696
Control A versus No treatment	0.31 ₁	0.758	−0.55 ₁	0.586
Control B versus No treatment and Control A	−0.36 ₁	0.716	−1.61 ₁	0.107

Statistical Analyses

To examine whether individual fruit set and percent leaf damage varied by exclusion treatment (five treatments), transect (three transects), and the interaction of treatment and transect, we used two separate generalized linear models (GLM) in the *MASS* package in R (Venables and Ripley 2002). Both treatment and transect were treated as fixed factors. We considered transect a fixed factor because there were only three transects and we chose them deliberately with respect to elevation. A negative binomial error distribution was used for both models because the response variables (number of set fruits and percent leaf damage) were overdispersed, and because this distribution provided the best fit to the data error structure and allowed for the use of pre-planned contrasts. In both models, we included pre-planned contrasts to specifically address study question 1 and 2 (contrast: *All animals excluded* versus all other treatments) and study question 3 (contrast: *Crawling insects excluded* versus *No treatment*, *Control A*, and *Control B*). Two additional preplanned contrasts were used to examine whether there was an effect of plastic flashing (contrast: *Control A* versus *no treatment*) or netting (contrast: *Control B* versus *No treatment* and *Control A*). Code for all analyses and raw data files are available from the Dryad Digital Repository (doi:10.5061/dryad.tr20q).

RESULTS

Fruit set marginally varied by exclusion treatment ($P = 0.078$) and transect ($P = 0.065$), but not the interaction of treatment and transect ($P = 0.857$) in a generalized linear model (Table 1A, Fig. 2A). Pre-planned contrasts demonstrated that animals caused a 42% reduction in fruit set on average compared to when all animals were excluded ($P = 0.007$; Table 1B). All other planned contrasts did not reveal significant differences among treatments, i.e., there

was no effect of crawling insects, plastic flashing or netting on fruit set (Table 1B).

Leaf damage significantly varied by exclusion treatment ($P = 0.008$), transect ($P = 0.012$), and by the interaction of treatment and transect ($P = 0.022$) in a generalized linear model (Table 1A, Fig. 2B). Pre-planned contrasts demonstrated that animals caused a 159% increase in leaf damage compared to when all animals were excluded ($P < 0.001$; Table 1B). All other contrasts were not significant, i.e., there was no effect of crawling insects, plastic flashing or netting on leaf damage (Table 1B).

DISCUSSION

We demonstrated that *Claytonia megarhiza* undergoes autonomous self-fertilization in the absence of pollinators at a single site in the central Sierra Nevada. Overall, reproduction appears to be negatively impacted by animals: there was a 42% reduction in fruit set and a 159% increase in leaf herbivory in the presence of animals. We found no evidence that ants or other crawling insects acted as either pollinators or herbivores, despite the prior observation that ants are floral visitors of this species in Yosemite National Park (Fig. 1).

Our results suggest that *C. megarhiza* may be predominantly self-fertilizing near its southern range edge in California. The evolution of self-fertilization is predicted to be greater in range edge and peripheral populations, which may suffer from marginal environmental conditions (Busch 2005; Herlihy and Eckert 2005; Moeller et al. 2012). For example, reduced or unfavorable growing seasons may necessitate shorter reproductive cycles, which favor self-fertilization or mixed mating to provide for reproductive assurance. Range edge populations may also experience greater mate- or pollinator-limitation, which also favor self-fertilization (Moeller and Geber, 2005; Moeller 2006; Moeller et al. 2012). For *C. megarhiza*, an alpine plant already subject to harsh environmental conditions, the range edge

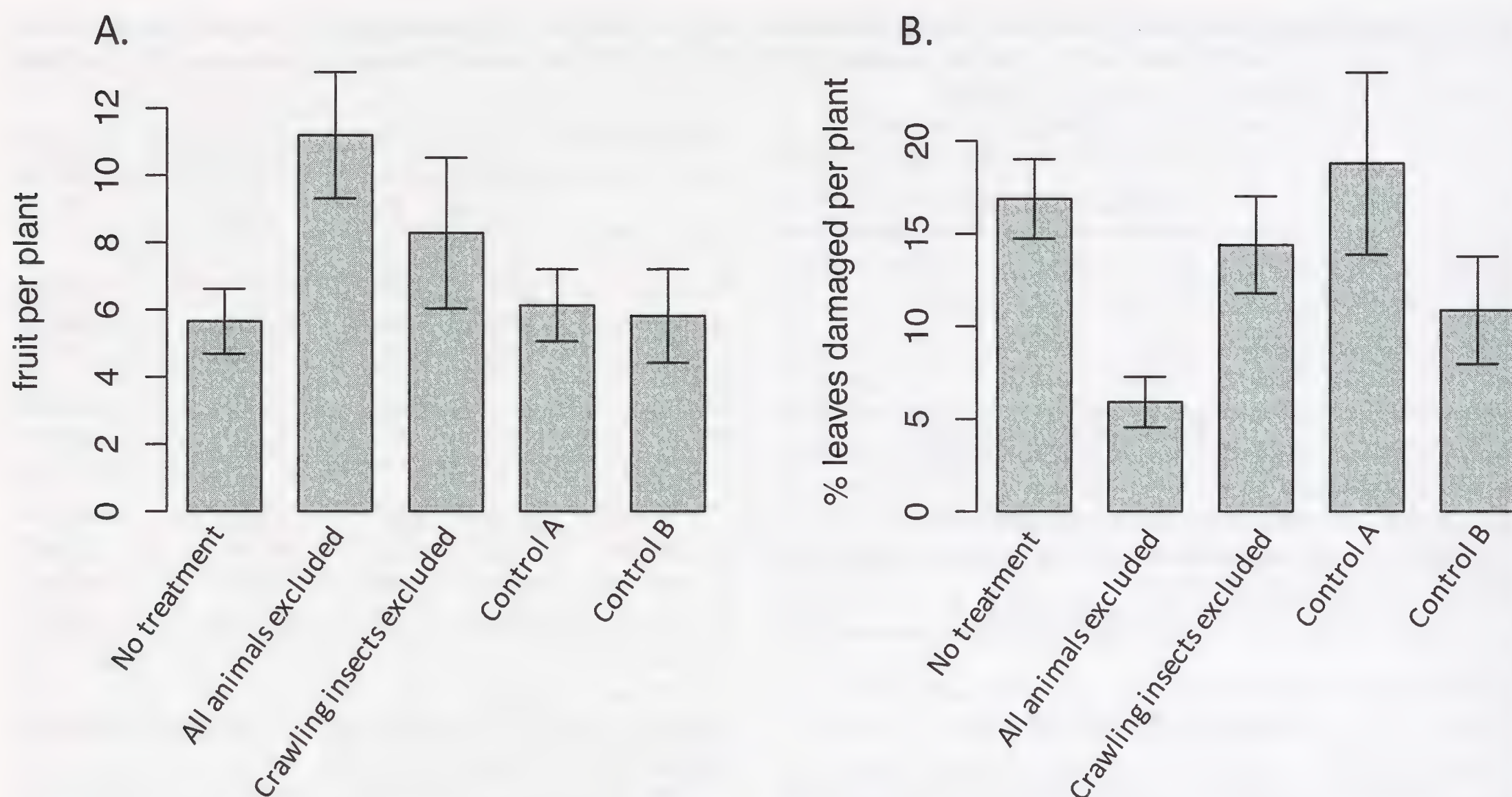


FIG. 2. Observed mean fruit set (A) and mean percent leaf damage (B) per exclusion treatment $\pm$ 1SE. Experimental treatments included: “No treatment” where plants were left unmanipulated; “All animals excluded” where netting, plastic flashing, and ‘Tree Tanglefoot’ impeded access by most insects and vertebrates; “Crawling insects excluded” where plastic flashing and ‘Tree Tanglefoot’ impeded access by ants and other crawling insects; “Control A” where plastic flashing without ‘Tree Tanglefoot’ allowed all animals to access plants; “Control B” where plastic flashing was covered with netting with holes to allow animals to access plants.

position may further challenge reproductive success and lead to the evolution of greater self-fertilization. Furthermore, *C. megarhiza* is reported to vary in ploidy among populations ($2n = 12, 16, 24, 32, 34, 36$; Baldwin et al. 2012), which could influence variation in breeding system as polyploidy is often associated with shifts to self-fertilization (Barringer 2007). Careful investigation of *C. megarhiza* in core and range edge habitats will help to better understand how these environments impact reproduction.

Consistent with increased self-fertilization at the study site, there appears to be reduced investment in pollinator attraction traits. We noted that petals of opened flowers at our study site were just 3–4 mm long, and are among the smallest reported for this species (e.g., a range of 5–9 mm is reported in Baldwin et al., 2012). Additionally, the petals were paler in color compared with those found in some northern populations (Grossenbacher, pers. obs.). A trend toward reduced floral investment following the evolution of predominant selfing has been found in many species (i.e., Sicard and Lenhard 2011). Nonetheless, some outcrossing may occur in this focal population, as our experimental design did not rule out potential for a mixed-mating strategy. For example, some cross-pollination may have occurred in treatments that permitted floral visitors, while delayed autonomous self-fertilization provided a backup mechanism in treatments where visitors were excluded. Determining the extent of cross-pollination near the southern range edge will require genetic data

to estimate rates of self-fertilization in untreated plants.

Knowledge of the reproduction of *C. megarhiza*, a rare species in California, can be used for management in several ways. When establishing new populations or restoring existing populations, the ability of this species to produce self-fertilized seed might allow for the successful establishment of relatively few individuals, as they will effectively produce seed without cross-pollination. Given the high rates of leaf herbivory and reduced fruit set in the presence of animals, temporary animal exclosures may help new plants to establish and boost reproductive output of existing plants. Finally, existing populations could be significantly differentiated from one another due to the rapid accumulation of genetic changes in predominantly selfing lineages and may exhibit high levels of fixed genetic load due to the accumulation of harmful mutations (reviewed in Wright et al., 2013). This may need to be taken into account if seed is to be transferred among populations or used to establish new populations.

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